
Systematics and Ecology of a New Species of Seagrass (*Thalassodendron*, Cymodoceaceae) from Southeast African Coasts

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ABSTRACT. Tropical seagrass communities are one of the most productive aquatic ecosystems on earth. A high diversity of seagrass species occurs in southeastern Africa; however, these marine angiosperms are among the least studied in the world. To address this, we have revised *Thalassodendron* Hartog (Cymodoceaceae), one of the most representative seagrasses in these coastal waters. Morpho-anatomical analyses, complemented with field data, reveal that specimens from rocky habitats present a number of distinguishing characters (e.g., rhizome internode lengths, leaf epidermal cells, and flower structures) that recommend their exclusion from the species *T. ciliatum* (Forssk.) Hartog. A new species from rocky habitats, *T. leptocaula* Maria C. Duarte, Bandeira & Romeiras, is thus described and illustrated, with the type from Mozambique, and an identification key for the investigated taxa is presented.

Key words: Coastal waters, Cymodoceaceae, IUCN Red List, seagrass, southeastern Africa, *Thalassodendron*.

Seagrass species are marine angiosperms widely distributed in both tropical and temperate coastal waters, creating one of the most productive aquatic ecosystems on earth (Gullström et al., 2002; Spalding et al., 2003). Seagrass meadows function as shelters and nurseries for juvenile animals. Their canopy acts as a hydrodynamic barrier in near shore areas, and their roots and rhizomes stabilize bottom sediments, providing large benefits for fisheries (e.g., Bandeira, 1995; Gullström et al., 2002; Spalding et al., 2003;

Eklöf et al., 2005). Seagrass beds also play an important role in the development of carbonate sediment facies, promoting the settling and stabilization of fine sediment; moreover, seagrass stems and blades provide important habitats for epiphytic marine organisms, such as calcareous faunas and crustose coralline algae, which ultimately contribute skeletal material to the substrate (Perry & Beavington-Penney, 2005).

Although seagrasses provide one of the most important coastal ecosystems, a decline in their distribution and abundance has been observed and is due to a growing coastal population and an over-exploitation of resources (e.g., Short & Wyllie-Echeverria, 1996; Barberá et al., 2005). Together with mangroves, coral reefs, and tropical rainforests, seagrass meadows are among the most threatened ecosystems on earth (Waycott et al., 2009). Seagrass meadows and the ecosystems they support are also threatened by natural disturbances and the potential impacts of climate change (Björk et al., 2008). The preservation of these ecosystems and their associated services—in particular, biodiversity, primary and secondary production, nursery habitat, and nutrient and sediment sequestration—should be a global priority (Orth et al., 2006). An ecosystem-based conservation and management strategy is essential to preserve not just seagrasses and their dependent communities, which include several threatened species, but also the entirety of coastal ecosystems (Orth et al., 2006; Hughes et al., 2009).

A high diversity of seagrass species occurs in southeastern Africa, which is recognized as one of the world's most important seagrass areas (Spalding et al., 2003).

An increasing loss of seagrass habitats was reported for southeast African coasts, namely for Mozambique, with ca. 2500 km of coastline. Estimates of seagrass areal coverage in Mozambique point to 439.04 km², of which 27.55 km² are reported as lost (Bandeira & Gell, 2003). About 12 species occur in this country (Bandeira & Gell, 2003), and diverse taxonomic questions remain to be solved.

Twelve seagrass genera are accepted worldwide: five in Cymodoceaceae (*Amphibolis* C. Agardh, *Cymodocea* K. D. Koenig, *Halodule* Endl., *Syringodium* Kütz., *Thalassodendron* Hartog); three each in Hydrocharitaceae (*Enhalus* Rich., *Halophila* Thouars, *Thalassia* Banks) and Zosteraceae (*Heterozostera* (Setch.) Hartog, *Phyllospadix* Hook., *Zostera* L.); and one in Posidoniaceae (*Posidonia* K. D. Koenig) (den Hartog & Kuo, 2006). Along southeast African coasts, most of the marine angiosperms belong to Cymodoceaceae. According to Tomlinson (1982), this family can be divided into two major groups. The first includes the genera *Cymodocea*, *Halodule*, and *Syringodium*, which are generally characterized by shedding leaf blades, persistent leaf sheaths, stalked anthers, and herbaceous rhizomes with monopodial branching. The second group includes the genera *Thalassodendron* and *Amphibolis* (the latter from the coasts of Australia), which are characterized by leaf blades and sheaths that shed together, subsessile anthers, viviparous reproduction, and woody rhizomes with sympodial branching.

In general, the root morphology that is characteristic of most seagrasses (i.e., an extensive rhizome system with additional anchorage function and dispersal by lateral growth) confines most species to soft-bottom habitats composed mainly of sand or soft substrates with shells or coral debris (den Hartog, 1970; Phillips & Meñez, 1988; Bandeira & Björk, 2001). Despite the fact that most of the Cymodoceaceae genera only occur on unconsolidated substrates, some species can be found in rocky substrates: *Amphibolis antarctica* (Labill.) Asch. and *A. griffithii* (J. M. Black) Hartog can be found along warm-temperate west and south Australian coasts, and *Thalassodendron pachyrhizum* Hartog can be found along warm-temperate west and southwest Australian coasts (den Hartog, 1970; Kuo & McComb, 1998; Short et al., 2001). The widespread *T. ciliatum* (Forssk.) Hartog, which occurs along tropical and subtropical coasts from the Red Sea eastward to the Asiatic coasts of the Pacific and the north Australian

coasts, and southward along the east African coasts, has been reported from both sandy and rocky habitats (Phillips & Meñez, 1988).

Morphological differences between southeast African *Thalassodendron ciliatum* populations in sandy and rocky habitats have been observed by several authors. Obermeyer (1966) compared populations from sheltered, warm coral reefs without wave action with populations from colder waters of sandstone rock crevices exposed to waves that are characteristic of south African habitats. The author observed that these specimens presented gnarled rhizomes, flexible stems, and thinner, narrower leaves, which were absent in populations from sandy substrates. In addition, Bandeira's studies (2002a, 2002b) on populations of *T. ciliatum* from rocky habitats with a very strong water current along southern coasts of Mozambique described morphological traits similar to those previously reported by Obermeyer (1966), e.g., thinner stems, fewer and narrower leaves, and shorter and more condensed internodes than specimens from sandy substrates. Furthermore, in rocky substrate specimens, the growth rate dynamics were quite different, with higher growth rates per unit area; an increase in leaf length and biomass per unit area was also higher in such plants (Bandeira, 2002b). High density of shoots per unit area in rocky habitats prompted these differences.

The morphological distinction between the *Thalassodendron ciliatum* specimens from sandy and rocky habitats relied on the vegetative structures, since reproductive specimens were only known in populations from sandy habitats in Mozambique (Bandeira & Nilsson, 2001; Bandeira, 2002b). Rocky and sandy populations were observed and sampled during the fieldwork performed in Mozambique, and for the first time (at the end of 2008) it was possible to collect individuals from rocky habitats with female reproductive structures. The extreme rarity of reproductive structures among *Thalassodendron* specimens from rocky habitats, confirmed within the context of studies on Cymodoceaceae for *Flora Zambesiaca* (Duarte, 2009), probably explains the current merging of rocky and sandy habitat specimens within the same taxon, though the differences in the morphological and physiological features between them are evident. The combination of morpho-anatomical analyses with field data presented here supports the recognition of two taxa within *Thalassodendron* specimens from southeast African coasts: *T. ciliatum* and *T. leptocaula* Maria C. Duarte, Bandeira & Romeiras.

Thalassodendron leptocaula Maria C. Duarte, Bandeira & Romeiras, sp. nov. TYPE: Mozam-

bique. Maputo: Matutuíne, Ponta do Ouro, 28 Nov. 2008 (♀), *M. C. Duarte & A. M. Manjate* 3801 (holotype, LISC; isotypes, LMU, MO). Figures 1, 2.

Haec species *Thalassodendron ciliato* (Forssk.) Hartog affinis, sed ab eo rhizomate usque ad 3 mm diametro, internodiis (0.5)1–6 mm longis, foliis lamina 3–9 cm longa et 3–7 mm lata, epidermidis cellulis pariete anticlinali flexuoso, floribus masculinis in bractea solitaria foliosa inclusis atque floribus femineis in bracteis 3 foliaceis inclusis differt.

Perennial, dioecious seagrass; rhizomes with sympodial branching, brown, terete, gnarled, to 3 mm diam.; vertical rhizomes rare; roots usually much branched, 2 at the stem-bearing internode (4th), 2 at the preceding internode (3rd), and none at the 1st and 2nd internodes; internodes much condensed (0.5–)1–6 mm. Scales ca. 5 mm, broadly ovate, early deciduous, dark brown; apex obtuse and apiculate; stems erect, 1(2), unbranched or little branched, to 70 cm, 1–2 mm width, with 4 or 5(6) leaves per shoot; leaf sheaths 10–30 × 3–9 mm, cuneate at the base, cream at the base becoming greenish (similar to leaf blade) to the top, with obtuse auricles, caducous, leaving circular scars irregularly spaced, to 10 mm apart; tanniniferous cells usually inconspicuous, margins scarious; ligule obtuse, 0.5–0.75 mm high; leaf blade usually falcate, 3–9 × 0.3–0.7 cm, greenish brown in dried condition; distal margins irregularly serrulate; veins (7)11 to 15(17), united below leaf apex; median and lateral veins slightly prominent; 15 to 23 rows of cells between secondary veins; leaf epidermis cells elongate and rectangular with anticlinal walls sinuous in surface view; leaf apex obtuse, slightly emarginate, denticulate, except at the middle zone; apical teeth to 0.5 mm high, acute or truncate. Squamules in leaf axils in 2 opposite groups of (1)2 to 4 squamules each, of unequal size, the longer about 0.75–2 mm. Male and female flowers solitary on short lateral shoots near the base of leaf clusters. Male flower enclosed in a leafy bract, sessile; anthers ca. 2.5 mm, 2 dorsally connate over entire length and attached at the same height with a short terminal appendage (ca. 0.5 mm), entire. Female flower enclosed in 3 leafy bracts, all differentiated into a sheath and a blade, with a ligule 0.5–0.75 mm; 1st bract outermost with a sheath 13–15 mm, the blade slightly smaller; 2nd bract with a sheath ca. 16–22 mm, the blade slightly shorter or longer; 3rd bract 14–20 mm, the blade equal to or longer, slightly falcate with the apex acute, obscurely veined, somewhat fleshy; ovary ellipsoid, 1.5–2 mm; style divided into 2 stigmatic arms 12–16 mm, strap-shaped. Seedlings viviparous.

Distribution and habitat. According to current data, *Thalassodendron leptocaule* occurs in southeast African tropical coastal areas from Xai-Xai (Gaza Province) and Ponta do Ouro (Maputo Province, type locality) in southern Mozambique, extending to Boteler Point (KwaZulu-Natal Province) in South Africa. Field observations (S. O. Bandeira) indicate the presence of the taxa in Chidenguele (70 km north of Xai-Xai) and north to Inhambane Province in Mozambique. *Thalassodendron leptocaule* occurs from the intertidal area to the subtidal fringe, usually in rocky pools, in crevices and creeks, and on calcareous sandstone, and is exposed to severe wave action. The species occurs in habitats that are permanently submerged or partially exposed at low water to ordinary spring tides (whereas *T. ciliatum* occurs from the lower intertidal to subtidal areas and always occurs with residual water or is submerged), and water temperature in the distribution area ranges between ca. 27°C (at Maputo latitude) and 26°C in the south (at Richards Bay latitude) during the warmest month (February). This species forms dense communities and is usually associated with seaweeds. Unlike *T. ciliatum*, the presence of epiphytic seaweeds along the stems is very rare. As in *T. ciliatum*, calcareous encrusters, such as crustose coralline algae and epiphytic fauna (Perry & Beavington-Penney, 2005), in stems and especially in leaves are common although much more expressive—512 g/m² versus 40 g/m² are referred (Bandeira, 2002b) to *Thalassodendron* plants in rocky and sandy habitats, respectively.

IUCN Red List category. Data on population size, structure, trend, and range for *Thalassodendron leptocaule* are insufficient, and only a conservation assessment of Data Deficient (DD; IUCN, 2001) can be made following the IUCN Standards and Petitions Subcommittee (2010). However, it should be noted that the particular habitat of this species is very limited along southeast African coasts and may be affected by threats, such as siltation, and continued growth of tourism infrastructures and activity in coastal areas.

Phenology. The flowering specimens of *Thalassodendron leptocaule* were gathered in October and November.

Etymology. The specific epithet *leptocaule* is from Latin and refers to the long and slender stems of *Thalassodendron leptocaule*.

Discussion. As summarized in Table 1, the *Thalassodendron ciliatum* specimens from sandy habitats



Figure 1. *Thalassodendron leptocaulle* Maria C. Duarte, Bandeira & Romeiras. —A. Community of *T. leptocaulle* and seaweeds in rocky pools, Inhaca Island, Ponta Mazónduè, Mozambique. —B. Flowering shoot with viviparous seedling (arrow). —C. Inner bract enclosing the female flower in fresh specimen. —D. Inner bract enclosing the female flower (*M. C. Duarte & A. M. Manjate 3801*, LISC). Scale bars: B = 15 mm; C, D = 5 mm.

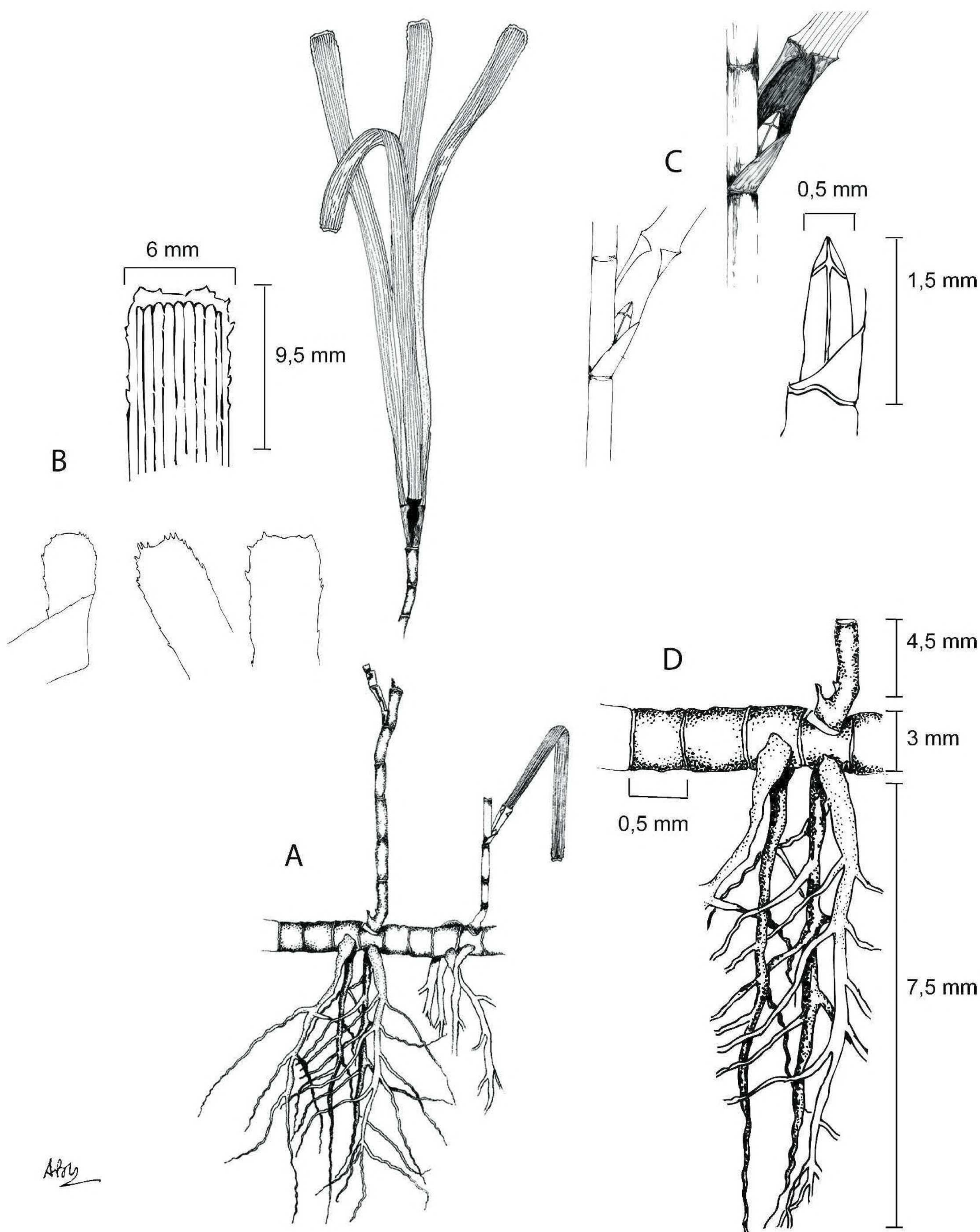


Figure 2. *Thalassodendron leptocaule* Maria C. Duarte, Bandeira & Romeiras. —A. Habit. —B. Leaf apices. —C. Male flower. —D. Rhizome. A, D drawn from Ward 9052 (K); B, C from Mauve & Verdoorn 71 (BM).

are distinctly different from *T. leptocaule* specimens from rocky habitats. Morpho-anatomical analyses indicated that leaf epidermal cells (either on adaxial or abaxial surfaces) are somewhat isodiametric or rectangular with straight anticlinal walls in *T. ciliatum* (Fig. 3A) and rectangular with sinuous anticlinal walls

in *T. leptocaule* (Fig. 3B) (a character also present in *Amphibolis*). The male flower in *T. ciliatum* is protected by four bracts rather than one, as is the case in *T. leptocaule*; anthers from *T. ciliatum* are considerably longer, 6–10 mm versus ca. 2.5 mm (Fig. 3C, D). The only male specimen known of *T.*

Table 1. Ecological and morpho-anatomical comparison between *Thalassodendron ciliatum* (Forssk.) Hartog (sensu Duarte, 2009) and *T. leptocaule* Maria C. Duarte, Bandeira & Romeiras; 73 specimens (housed in BM, K, LISC, LMU, PRE, and SRGH), 33 from rocky habitats and 40 from sandy habitats, were examined. Data concerning substrate type (rocky and sandy) were taken from herbarium labels.

Character	<i>T. ciliatum</i>	<i>T. leptocaule</i>
Substrate	sandy	rocky
Rhizomes	reddish brown, angled, to 8 mm diam.; with vertical rhizomes; internodes 0.5–3 cm	brown, terete, to 3 mm diam.; vertical rhizomes rare; internodes (0.05–)0.1–0.6 cm
Roots	little or much branched; root hairs common; roots to 10 at the stem-bearing internode (4th) and at the preceding internode (3rd), none at the 1st and 2nd internodes	usually much branched; root hairs rare; roots 2 at the stem-bearing internode (4th), 2 at the preceding internode (3rd), and none at the 1st and 2nd internodes
Stems	to 35 cm long, 1.5–3.5(–4) mm wide	to 70 cm long, 1–2 mm wide
Leaf scars	to 20 mm apart at the base; the upper successively closer to 1–2 mm apart	irregularly spaced, to 10 mm apart
Ligule	obtuse, 1–1.5 mm high	obtuse, 0.5–0.75 mm high
Leaves	(5)6 to 8(9) per shoot, 5–15 cm long, 5–14 mm wide; blade margins serrulate	4 or 5(6) per shoot, 3–9 cm long, 3–7 mm wide; blade margins ± serrulate
Leaf apex	obtuse, slightly emarginate, denticulate; apical teeth to 0.5–1 mm high	obtuse, slightly emarginate, denticulate, except at the middle zone; apical teeth to 0.5 mm high
Leaf epidermal cells (in surface view)	somewhat isodiametric or rectangular; anticlinal walls straight; 25 to 35(40) cell rows between secondary veins	rectangular; anticlinal walls sinuous; 15 to 23 cell rows between secondary veins
Leaf veins	5 to 29	(7)11 to 15(17)
Flower arrangement	on short lateral shoots near the base of leaf clusters	on short lateral shoots near the base of leaf clusters
Flower structure	flowers (male and female) enclosed by 4 leafy bracts	flowers enclosed by 1 (male) or 3 (female) leafy bracts
Female flower	style divided into 2 slender, stigmatic arms 20–30 mm; apex of the inner bract (4th bract) obtuse	style divided into 2 stigmatic arms 12–16 mm; apex of the inner bract (3rd bract) acute
Male flower	2 anthers dorsally connate over entire length and attached at the same height; anthers 6–10 mm, with a short terminal appendage, sometimes bilobed	2 anthers dorsally connate over entire length and attached at the same height; anthers ca. 2.5 mm, with a short terminal appendage, entire

leptocaule (Mauve & Verdoorn 71, BM) was carefully examined to put forward the hypothesis that eventual bracts could leave scars from shedding, though the material was not dissected to avoid damage to the specimen. The female flower in *T. ciliatum* is enclosed by four bracts (the inner one without a ligule and with the apex obtuse), whereas in *T. leptocaule*, it is enclosed by three bracts (the inner one with a ligule and with the apex acute, see Fig. 1C, D). Common characteristics for both species include the presence of a woody rhizome with sympodial branching and woody roots with stems arising at every fourth internode. The leaf blade and sheath shed simultaneously; anthers are connate over their whole length; and viviparous seedlings are present.

It has to be noted that some of the morphological characters used to distinguish the two *Thalassodendron* taxa (see Table 1) are also useful taxonomic characters for distinguishing other seagrass species, e.g., the organization of the rhizomes and variation in

the erect shoots (Posluszny & Tomlinson, 1991) or the shape of epidermal cells (Kuo & Stewart, 1995; Kuo & den Hartog, 2006). In effect, features of the epidermis are useful characters in systematic botany (Stace, 1980), and as stated in a recent study by Liu and Zhu (2009), the shape of epidermal cells and the pattern of anticlinal walls are variable in different taxa but consistent within the same taxon.

Bandeira and Nilsson (2001) performed a genetic study of population based on random amplification of polymorphic DNA (RAPD) markers that found scarce differences among sandy and rocky populations of *Thalassodendron* specimens from southern Mozambique. However, this study was based on an insufficient number of random primers and was not conclusive to generate the genomic fingerprint distinctive for *Thalassodendron* species.

Furthermore, the genetic analyses of other seagrass genera were inconclusive. Genetic data from specimens of *Zostera marina* L., *Z. asiatica* Miki, and *Z.*

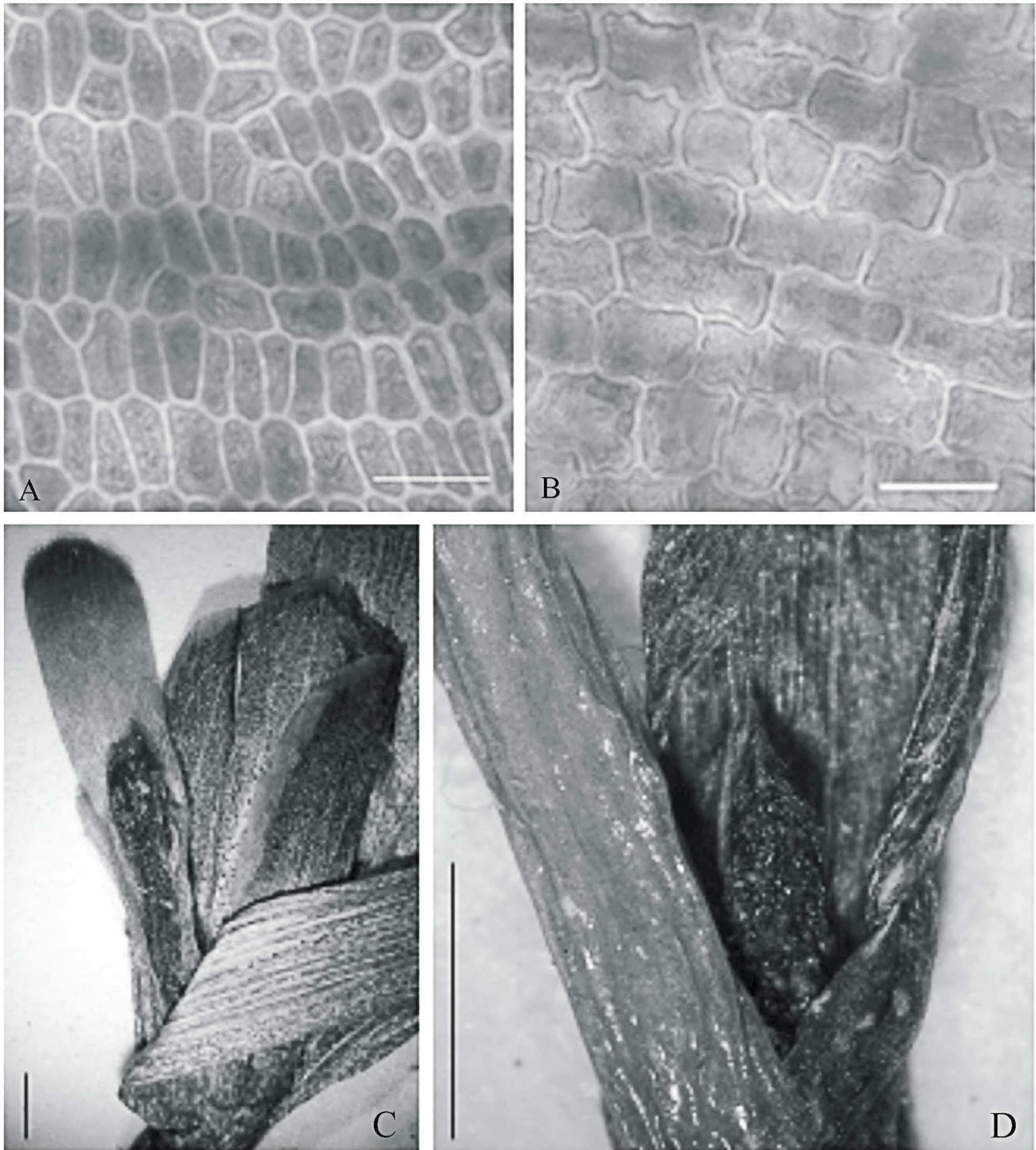


Figure 3. A, B. Comparison of leaf epidermis cells. —A. *Thalassodendron ciliatum* (Forssk.) Hartog, the leaf epidermis showing isodiametric or rectangular cells with straight anticlinal walls (Mogg 35185, LISC). —B. *T. leptocaulle* Maria C. Duarte, Bandeira & Romeiras, the leaf epidermis revealing elongate, rectangular cells with sinuous anticlinal walls (Mogg 31525, LISC). C, D. Comparison of stamens. —C. *T. ciliatum* (Moss 20794, K; reproduced with kind permission of the Board of Trustees of the Royal Botanic Gardens, Kew). —D. *T. leptocaulle* (Mauve & Verdoorn 71, BM; reproduced with kind permission of the Head of Collections of the Department of Botany of the Natural History Museum, London). Scale bars: A, B = 25 μ m; C, D = 2 mm.

japonica Asch. & Graebn. from Pacific coasts of North America and Asia (Japan) revealed species boundaries that were not congruent with morphological traits (Talbot et al., 2006), recommending integrative taxonomic studies.

Some hypotheses may explain the discrepancy between genetic and morphological analyses, namely, phenotypic plasticity, morphological convergence, or

interspecific hybridization. Presently, DNA barcoding is well suited to address species identification quickly and accurately for many plant groups, although the two regions of plastid DNA (*matK* and *rbcL*) that have been selected (CBOL Plant Working Group, 2009) as such plant barcodes have revealed relatively few differences between the barcodes for closely related species. Therefore, it is expected that

in the near future, the use of other DNA regions (e.g., nuclear low-copy genes) should permit the identification of hybrids and also overcome the lower levels of discrimination, providing a more comprehensive picture of seagrass evolution.

Despite some taxonomic controversies associated with the relationships within seagrass species, it is suggested that *Thalassodendron* species are undergoing an adaptive radiation in southeast African coasts, driven in part by local adaptation to the ecological heterogeneity of soils. In conclusion, the morphological and anatomical analyses presented in this paper highlight the fact that the seagrass populations of sandy habitats (*T. ciliatum*: see Fig. 3A, C) are well differentiated from the populations of rocky habitats (*T. leptocaule*: see Figs. 1, 3B, D).

KEY TO *THALASSODENDRON* SPECIES IN SOUTHEAST AFRICA

- 1a. Rhizomes to 8 mm diam.; internodes 0.5–3 cm long; stems 1.5–3.5(–4) mm wide; leaves (5)6 to 8(9) per shoot, 5–15 cm long, 5–14 mm wide; epidermal cells with straight anticlinal walls *T. ciliatum*
- 1b. Rhizomes to 3 mm diam.; internodes (0.05–)0.1–0.6 cm long; stems 1–2 mm wide; leaves 4 or 5(6) per shoot, 3–9 cm long, 3–7 mm wide; epidermal cells with sinuous anticlinal walls *T. leptocaule*

Paratypes. MOZAMBIQUE. **Maputo:** Matutuíne, Inhaca Island, 30 Oct. 1962 (♂), *Mauve & Verdoorn* 71 (BM); 23 mi. E of Maputo, 20 July 1956, *Mogg* 31525 (BM, K, LISC, PRE, SRGH). SOUTH AFRICA. **KwaZulu-Natal:** Hlabisa, 2.9 km N of Boteler Point, 22 Oct. 1976, *Ward* 9052 (K, PRE).

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